

MORTALITY FACTORS, POLLEN UTILIZATION, AND
SEX RATIO IN *MEGACHILE PUGNATA* SAY
(HYMENOPTERA: MEGACHILIDAE),
A CANDIDATE FOR COMMERCIAL
SUNFLOWER POLLINATION

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Abstract.—Data on the nesting biology of *Megachile pugnata* was obtained from 359 trap-nests at two sites in northern Utah. Bees made an average of 3.8 cells per nest and provisioned cells exclusively with pollen from the Compositae. Approximately 12% of all offspring were killed by either the clerid predator *Trichodes ornatus* or the chalcid parasite *Melittobia* sp. An additional 30–38% of offspring failed to complete development to the adult stage. Most of this immature mortality occurred during the overwintering and incubation stages. The sex ratio of the populations varied between 1.4 to 1.8 ($\delta/\text{♀}$). Nests with with 3 or fewer cells had a lower percentage of male offspring than all other nests combined. It may be possible to increase the percentage of female bees by decreasing the depth of the nesting hole.

Introduction

Megachile (Sayapis) pugnata Say is a gregariously nesting leafcutting bee distributed throughout most of the United States and southern Canada (Hurd 1979). The species commonly nests in pre-existing holes in wood and readily accepts sumac trap-nests (Medler 1964) or artificial wooden domiciles as nesting sites. The potential importance of *M. pugnata* as a pollinator in commercial sunflower fields has recently been recognized (Parker 1981) and is currently under study (Parker and Frohlich unpubl.).

Relatively little information is available on the biology of this potentially manageable species. Medler (1964) reported on the nest architecture and nest associates found in 20 sumac trap nests in Wisconsin. Parker (1981) and Hurd (1979) noted that *M. pugnata* visits a variety of flower species, but Hurd (1979) suggested that composite species are preferred. These records are based on flower visitations only; actual pollen usage has not been examined.

In this paper we report on mortality factors, pollen usage and sex ratio from 359 nests obtained from artificial domiciles at two sites in northern

Utah. Of especial interest is the relationship between mortality factors, sex ratio and number of cells per nest. Information on these parameters enable us to make suggestions regarding the size of nesting materials that might be offered to populations in commercial sunflower fields so as to minimize mortality and increase the percentage of females.

Methods

Nests of *M. pugnata* were obtained from trap-nest blocks placed at two sites in Cache Co. in northern Utah. The Faust site (42 km south of Logan, Cache Co., Utah, 1,800 m elevation) is on a hillside with a SW exposure. It is covered by large stands of mature aspen (*Populus tremuloides*) which are surrounded by open, grassland meadows. The Blacksmith Fork site (27 km SE of Logan, 1,500 m elevation) is on a canyon floor surrounded by maple-box elder with an understory of *Hydrophyllum*, *Cirsium* and *Balsamorhiza*. Trap-blocks were made of pine wood, and contained 50 drilled holes into which paper soda straws were inserted (7 mm diameter, 15 cm deep). Blocks were attached to dead trees with holes oriented horizontally.

Blocks were collected during the first week of July and maintained at room temperature in the laboratory until 1 September when nests were dissected. During dissection we recorded the contents of each cell, causes of mortality, and prepared pollen slides (Beattie 1971) from uneaten provisions or from pollen adhering to the cell walls. Live larvae were put into gelatin capsules and maintained at 4°C from 30 September until 9 June when they were incubated at 29°C. Adults were weighed upon emergence and released in a commercial sunflower field (Parker and Frohlich unpubl.).

Results

We recovered 359 completed and plugged *M. pugnata* nests from the two sites (165 Blacksmith Fork, 194 Faust). The sites differed significantly in the distribution of nests by cells per nest (χ^2 contingency tables, $\chi^2 = 12.59$, $df = 6$, $P = 0.05$): Blacksmith Fork nests averaged fewer cells per nest (3.5, SD 1.5) than did Faust nests (4.1, SD 1.6) (Fig. 1a). Overall, average cells per nest (3.8, SD 1.6) was similar to Medler's (1964) findings for holes of the same depth.

In contrast to Medler's (1964) report that *M. pugnata* is univoltine in Wisconsin, Utah populations had a partial second generation that emerged during the last half of August. Parker and Frohlich (unpubl.) also found a partial second generation in Utah populations. The sites differed in the percent of total offspring that emerged rather than entering diapause: Faust had significantly fewer emergent bees (3.3%) than did Blacksmith Fork (7.3%) ($\chi^2 = 8.90$, $P < 0.005$). There was rarely more than one emergent individual per nest.

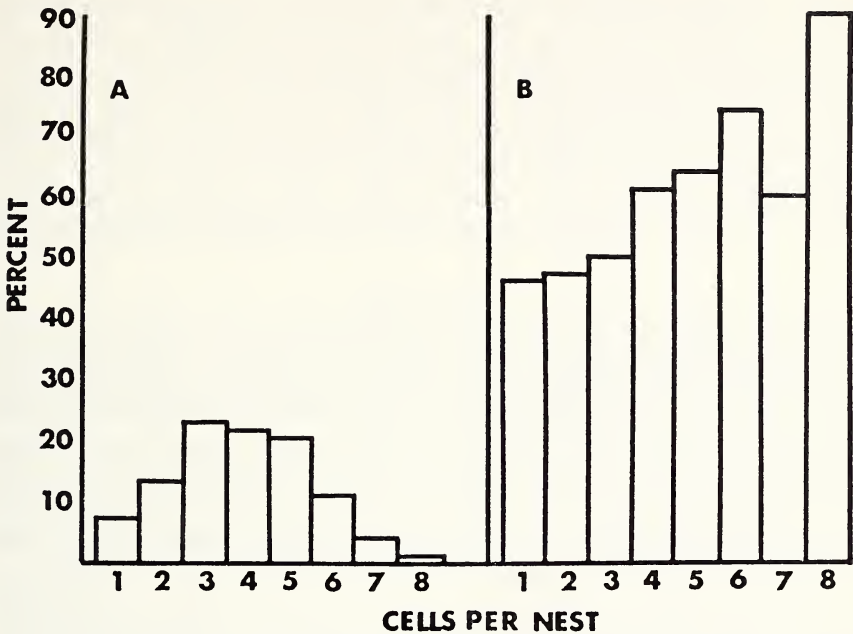


Fig. 1. a. Percent frequency distribution of nests by number of cells per nest. b. Percent of live adults that were males by number of cells per nest. Both sites combined for each figure.

Mortality factors.—Mortality factors included developmental arrest in all stages and various predators and parasites (Table 1). Mortality was significantly higher at Blacksmith Fork than at Faust ($\chi^2 = 8.8$, $P < 0.005$) and this was primarily due to the larval and sib caused categories. The latter category requires clarification. Bees that developed directly to the adult stage without an intervening period of diapause, destroyed any siblings between themselves and the nest entrance when they emerged. Apparently, egress could be achieved only at the expense of nest-mates. The higher percentage of emergent bees at Blacksmith Fork caused a significantly higher incidence of sib caused mortality at that site than at Faust ($\chi^2 = 36.9$, $P < 0.001$).

Most immature mortality occurred during larval and pupal stages: a smaller proportion of cells contained provisions but no egg, or unhatched eggs (Table 1). Most of the larval and pupal mortality was sustained during the overwintering and incubation treatments (Faust, larval 55.1%, pupal 88.3%, Blacksmith Fork, larval 64.0%, pupal 77.8%) and may have been due to maintenance at inappropriate temperatures (see also Medler 1964). The incubation treatment appeared to be especially detrimental to females; significantly more females than males died as pupae or adults during incubation (Faust, $\chi^2 = 12.2$, $P < 0.001$; Blacksmith Fork, $\chi^2 = 6.5$, $P < 0.02$).

Table 1. Percent mortality by stages in the life cycle due to developmental arrest or to parasites and predators (PP). Sib caused mortality was due to emergence of a partial second generation. Based upon 827 cells (Faust) and 579 cells (Blacksmith Fork).

	Provision	Dead egg	Larvae	Pupae	Adult	PP	Sib caused	Σ mortality
Faust	4.1	4.4	8.6	9.3	1.8	12.7	0.7	41.6
Blacksmith Fork	1.9	5.2	14.9	6.2	3.3	11.7	6.4	49.6

Predators and parasites destroyed approximately 12% of the cells at each site. Most of this mortality was caused by clerid beetles (*Trichodes ornatus*, 47.6% Faust, 71.2% Blacksmith Fork) and the chalcid parasite *Melittobia* sp. (39.1% Faust, 18.2% Blacksmith Fork). Small percentages of cells were destroyed by the chalcid *Monodontomerus* and the cuckoo bee, *Coelioxys alternata* Say. *Melittobia* and *Coelioxys* were also recorded by Medler (1964).

We compared the incidence of mortality among nests with different numbers of cells to determine if mortality was associated with nest size. Nests from both sites were combined and then grouped by number of cells. Numbers of dead and live individuals were then tabulated for each nest size category. No association between nest size and mortality was found ($\chi^2 = 6.53$, $df = 5$, $P > 0.25$).

Sex ratio.—*Megachile pugnata* is a markedly dimorphic bee: using weights as an estimate of body size gave a ♀/♂ size ratio of 1.82 (\bar{x} ♂ = 62.7 mg, SD 9.8, N = 65, range = 41.0–84.7; \bar{x} ♀ = 114.3 mg, SD 20.3, N = 74, range = 69.5–165.7). The expected sex ratio for the population was thus, 1.82 ♂ : 1 ♀ (Torchio and Tepedino 1980). The sex ratio of live offspring at Faust (1.76) did not differ from the expected value ($\chi^2 = 0.08$, $P > 0.75$) but the sex ratio at Blacksmith Fork (1.37) was significantly biased towards females ($\chi^2 = 5.55$, $P < 0.025$). These results were unchanged when dead but sexable individuals were included in the tests.

We examined the occurrence of male and female individuals in nests by grouping nests with the same number of cells for both sites and then tabulating the number of males and females at each cell position. All nest sizes (2 to 6 cells/nest; too few 7 and 8 cells available for statistical testing) had significantly more females in inner cells and more males in outer cells (χ^2 tests, all $P < 0.005$ or less). Thus, *M. pugnata* is similar to the alfalfa leaf-cutting bee, *M. rotundata* (Fabr.) (Stephen and Osgood 1965) and other megachilid bees (Krombein 1967) in the placement of males and females in the nest.

There was a significant association between the sex ratio and cells per nest (Fig. 1b). Nests with 1–3 cells had lower percentages of males (48.7%) than did nests with ≥ 4 cells (65.5%) ($\chi^2 = 17.1$, $P < 0.001$). Thus, as cells are

added to three-celled nests, there is a much greater probability that they will be males than females.

Pollen utilization.—We examined pollen samples from 1,203 cells at both sites. Few cells contained anything other than composite pollen, although the presence of more than one species of composite was not uncommon. In all, only 0.6% of all pollen grains at Faust and 2.5% at Blacksmith Fork were of non-composite species. It seems clear that the preferred pollen of this species, at least in northern Utah, is of the Compositae.

Discussion

Megachile pugnata possesses several characteristics in common with the semi-domesticated pollinator of alfalfa, *M. rotundata*, which make it an excellent prospect for the pollination of commercial sunflowers. The species is widespread in occurrence, accepts man-made nesting materials and populations are readily obtainable from appropriate habitats (Parker and Frohlich unpubl.). The species can also be manipulated through temperature treatments to ensure synchronization of emergence with sunflower anthesis. In addition, Utah populations appear to exclusively collect the pollen of composites.

Additional work is required to determine the most appropriate temperature at which overwintering bees should be held and subsequently incubated so as to reduce mortality. This is particularly important because the data suggest that females, which are more valuable as pollinators than males, are more susceptible to the temperature treatments employed here. Some of this mortality may be unavoidable, however, because it is necessary to hold bees at cold temperatures beyond their "normal" emergence times (June) to synchronize their emergence with sunflower bloom in mid-July.

The depth and diameter of nesting holes influences the number of cells made per nest and the sex ratio of the alfalfa leafcutting bee, *M. rotundata* (Stephen and Osgood 1965; Gerber and Klostermeyer 1972). A similar effect is likely for *M. pugnata*. Although we have no data on the influence of different diameter holes, it is likely that a decrease in the depth of holes from the 15 cm used here, to 7.5 cm, would result in an increase in the percentage of female offspring. As Stephen and Osgood (1965) found for *M. rotundata*, *M. pugnata* uses 15 cm holes inefficiently: only 3 to 4 cells were made in most nests and much unutilized space remained. In addition, nests with 4 or more cells had significantly more males than nests with fewer cells (Fig. 1b). Thus, when space was more completely utilized, it was allocated to the less valuable (from the viewpoint of pollination) males. It is possible that a reduction in depth of nesting holes would increase the proportion of nests with fewer cells and thereby increase the percentage of female offspring. Whether or not such a procedure would reduce the total number of offspring

produced because of increased time spent in plugging shallower nests with fewer cells, and in searching for new nesting holes (Stephen and Osgood 1965), needs to be studied.

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